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**Guinea pig (*Cavia porcellus*) drinking preferences: Do nipple drinkers
compensate for behaviourally deficient diets?**

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Meiner Familie

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Summary

When offered hay ad libitum, rabbits prefer open dishes, but whether this preference applies in small rodents is unknown. We tested the drinker preference of 10 guinea pigs when offered open dishes (OD) and nipple drinkers (ND) simultaneously, and measured the amount of water consumed on four different diets (grass hay 100%, or as 10% of intake on diets of fresh parsley, seed mix, or pelleted complete feed, respectively) on either drinking system. All animals ingested the hay portion of the diets first. Individual animals differed significantly in the amount of drunk water. Less water was drunk on parsley than on the other diets. Nine of 10 animals clearly preferred ND when having a choice, and eight of these drank more when on ND only. On hay, similar amounts of water were drunk when on OD or ND only. Differences in water intake were reflected in urine production. Because drinking from ND in guinea pigs involves jaw movements similar to those in chewing, the results could suggest that when motivation for oral processing behaviour is not satisfied by a diet, animals may respond in using ND beyond physiological water necessity. Whereas physiological water requirements are probably better investigated with other drinking systems (possible overestimation when using ND), offering ND to pet guinea pigs most likely offers a form of behavioural enrichment that at the same time may increase water intake and hence act as prophylaxis against urolithiasis.

Zusammenfassung

Kaninchen bevorzugen Offentränke bei Heufütterung; ob dies bei Nagern zutrifft, ist unbekannt. Hier wird die Tränkepräferenz von 10 Meerschweinchen untersucht bei parallelem Angebot von Offen- (OT) und Nippeltränke (NT). Zusätzlich wurde der Wasserkonsum bei vier Diäten (Grasheu 100%, oder zu 10% der Futteraufnahme bei frischer Petersilie, Körnermischung und Pellets) für beide einzeln angebotenen Tränken gemessen. Alle Tiere frassen zuerst den Heuanteil. Die einzelnen Tiere unterschieden sich signifikant in der Tränkeaufnahme. Bei Petersilie wurde am wenigsten getrunken. Neun der zehn Tiere bevorzugten die NT, wenn sie die Auswahl hatten und acht dieser Tiere tranken mehr wenn die NT allein angeboten wurde. Der Unterschied zwischen den Tränken war nicht gleich bei allen Diäten: bei reiner Heudiät wurde gleich viel aus OT und NT getrunken. Die Unterschiede bei der Wasseraufnahme zeigten sich gleichermassen in der Urinproduktion. Da beim Trinken aus der NT ähnliche Kieferbewegungen wie beim Kauen ausgeführt werden, könnten diese Resultate anzeigen, dass bei mangelnder oraler Beschäftigung die NT über die physiologisch benötigte Wassermenge hinaus genutzt wird. Während der Wasserbedarf wahrscheinlich besser mit anderen Tränken untersucht wird (evtl. Überschätzung bei NT), könnte die NT bei Hausmeerschweinchen eine Verhaltensanreicherung sein, welche zugleich die Tränkemenge steigert und somit zur Prophylaxe der Urolithiasis beitragen kann.

ORIGINAL ARTICLE

Guinea pig (*Cavia porcellus*) drinking preferences: do nipple drinkers compensate for behaviourally deficient diets?

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Summary

When offered diets with hay *ad libitum*, rabbits (*Oryctolagus cuniculus*) clearly prefer open dishes over nipple drinkers, but whether this preference also applies in guinea pigs (*Cavia porcellus*) is unsure. We tested the drinker preference of 10 guinea pigs when offered open dishes (OD) and nipple drinkers (ND) simultaneously and measured the amount of water consumed by each animal on four different diets (grass hay 100%, or as 10% of intake on diets of fresh parsley, seed mix or pelleted complete feed, respectively) on either of the drinking systems. All animals ingested the hay portion of the combined diets first. The amount of water consumed differed significantly between individual animals. Animals drank less water on parsley than on the other diets. Nine of 10 animals clearly preferred ND when having a choice, and eight of these drank more when on ND only. The difference between the drinking systems was not consistent across all diets: on hay, similar amounts of water were drunk when on OD or ND only. Differences in water intake were reflected in urine production. Because drinking from ND in guinea pigs involves jaw movements similar to those in chewing, the results could suggest that when motivation for oral processing behaviour is not satisfied by a diet, animals may respond in using ND beyond physiological water necessity. Whereas physiological water requirements are probably better investigated with other drinking systems due to a possible overestimation when using ND, offering ND to pet guinea pigs most likely offers a form of behavioural enrichment that at the same time may increase water intake and hence act as prophylaxis against urolithiasis.

Keywords rodent, preference, feed intake, water intake, urine, stereotypy

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Introduction

Guinea pigs (*Cavia porcellus*) are popular domestic animals and therefore often presented in veterinary practices. Urolithiasis was among the top ten diagnoses for guinea pigs presented to a specialized exotic animal service (Langenecker et al., 2009), and the most frequent reason for telephonic inquiries at a nutritional consultancy service (Wolf and Kamphues, 2009). Because uroliths are commonly composed of calcium carbonate (Hawkins et al., 2009; Osborne et al., 2009), the pre-disposing factor is often suggested to be the guinea pig's calcium metabolism. Like the majority of the hindgut-fermenting herbivores (Hagen et al., 2015), guinea pigs absorb most of the ingested calcium from the gut and excrete the excessive calcium with the urine (O'dell et al., 1957).

Therefore, an excessive dietary calcium intake can have an impact on the formation of urinary stones, and a reduction of feed high in calcium is often recommended in literature (Kamphues, 1991; Wolf et al., 2008; Jepson, 2009; Samour, 2012).

In addition, the water intake plays an important role in the pathogenesis of urolithiasis. Insufficient water intake will lead to decreased urinary output and therefore more concentrated urine, which is related to an increased risk of urinary concretions (Wolf, 1959; Wolf et al., 2008). Because guinea pigs do not adapt to water deprivation, and their ability to concentrate urine is even less marked than in rats, drinking water should be available at all times (Dicker and Heller, 1951; Dutch and Brown, 1968).

In any species, water intake depends on various factors. Wolf et al. (2008) showed a strong

correlation between water consumption and feed intake, with a ratio of 2–4 ml water per ingested gram dry matter in guinea pigs and rabbits. Zentek et al. (1996) reported higher amounts of drinking water in guinea pigs fed on roughage, similar to observations of an increased water intake in rabbits fed on hay (Tschudin et al., 2011b; Prebble and Meredith, 2014). Furthermore, the choice of the drinking system plays an important role. Tschudin et al. (2011a) demonstrated a clear preference of rabbits for open dishes as compared to nipple drinkers; additionally, with restricted water access, the water intake from open dishes was significantly higher compared to nipple drinkers. Whether similar drinking preferences exist in guinea pigs is unsure. In a preliminary study with six animals on a diet of lucerne hay and pelleted lucerne (Hagen et al., 2014), guinea pigs did not show a specific preference to either drinking system, in contrast to chinchillas (*Chinchilla lanigera*) which clearly preferred the open dishes.

In this study, we investigated the water intake from nipple drinkers and open dishes in guinea pigs. We expected that, in contrast to the previous study (Hagen et al., 2014), with longer adaptation and a variety of diets, animals would display a preference for the open dishes, because they allow a faster and hence putatively more convenient water intake (Tschudin et al., 2011a). In contrast to the expectation, we found that guinea pigs preferentially used the nipple drinkers; our findings indicate that this may be linked to the fact that nipple drinkers offer an outlet for oral activity that may be related to the feeding mechanism in these animals.

Methods

This experiment was approved by the Animal Care and Use Committee of the Veterinary Office of Zurich (Nr. 260/2014). Twelve adult guinea pigs (mean \pm SD body mass 912 ± 40 g) of different ages (1- to 5-year old), sex (four intact and two castrated males, six intact females) and breed were used in this study. All animals came from the same private owner and had been used to nipple drinkers at the facility where they were usually kept in groups and outdoor enclosures. Prior to the study, all animals underwent a clinical examination and were considered clinically healthy. During the course of the experiment, one animal developed a mandibular abscess (considered unrelated to this study) and was completely excluded from the experiment. All animals were returned to their owner after the experiment.

Animals were adapted during 25 days to the experimental conditions; drinking water was provided by both open dishes and nipple drinkers during this period. Then, the experiment began in which each animal received all diets in a random sequence. A diet period started with an 11-day adaptation period followed by 4 days in metabolism cages for one drinking system (open dish or nipple drinker), and an identical sequence for the other drinking system. Air temperature was measured daily. During the adaptation periods, the animals were housed indoors at 21–24 °C. They were kept individually in enclosures whose walls had several holes (diameter of 2 cm) to allow contact to neighbour animals. The floor was covered with sawdust and each animal had a shelter. Water was first provided simultaneously from a round ceramic open dish (10 cm in diameter \times 5 cm in height) and a nipple drinker (Classic, large bunny, Pet Products, Caldex, Halifax, UK; clear plastic, 18 cm height, 6.5 cm diameter, max. content 6.2 dl, diameter on the metal nipple: 7 mm; height of the nipple above ground 8 cm) for each animal. The water was changed daily. A vitamin C supplement (Redoxon, Bayer, Basle, Switzerland) was dissolved in the water to yield 0.3 mg vitamin C per ml, and this solution was used to fill dishes and drinkers. The metabolism cages (153 cm length \times 43 cm width \times 40 cm height) had a perforated metal floor and were in a room at 21–28 °C. These cages were divided lengthwise in the middle by a sheet of clear plexiglass with holes, to house two animals per cage. Each compartment contained a tinted plexiglass shelter. Feed and water was offered in plastic dishes (8 \times 8 \times 2 and 15 \times 8 \times 2 cm, respectively) or in the nipple drinkers as mentioned above. Faeces and urine were separated below the cage floor by a fine wire mesh, collected for each individual twice daily to minimize urine evaporation losses and weighed.

During days 5–9 of the adaptation period, the water intake from both drinking systems offered in parallel was measured. During days 10–11 of an adaptation period, only the drinking system was offered that was used in the subsequent metabolism cage phase. After the metabolism cage phase, another 11-day adaptation period with water intake measurement at days 5–9 followed, and then the other drinking system was offered at days 10–11 and during the subsequent metabolism cage phase. Subsequently, the next diet was tested, until all animals had received all diets. The sequence of diets fed, and of drinking systems within diets, was randomized for all animals.

Four diet items were used – grass hay, fresh parsley, a commercial seed mix (Vita balance,

Meerschweinchen und Hamster, Landi Schweiz AG, Dotzigen, Switzerland) and a commercial pelleted guinea pig diet (Cavia Complete, Versele Laga, Deinze, Belgium). The nutrient composition of the diet items is compiled in Table 1. One diet consisted of grass hay only; the other diets consisted of one of the other diet items, with an additional offer of grass hay at 10% of the estimated dry matter intake.

Each day, the animals were checked for general condition, urination and defecation. It was also noted subjectively what feed the animals appeared to prefer by ingesting it first (hay or the other diet component). Water intake was measured as the difference of water offered and water leftovers. To account for evaporation losses, an additional open dish and an additional nipple drinker were placed each day in the same room. No evaporation loss was detected for nipple drinkers, and for open dishes, they averaged at 13.4 ± 3.9 g per day. The unavoidable dripping losses when placing the nipple drinkers were measured as described by Hagen et al. (2014) by weighing the filled nipple drinker, placing it in its position in the cage, removing it immediately and weighing it once more, before placing it again in its position for the day. These dripping losses averaged at 1.7 ± 1.1 g per placement. Whereas open dishes were never contaminated in the metabolism cages, contamination of open dishes occurred in the adaptation compartments and

was scored on a daily basis as 0 (no contamination), 1 (mild contamination), 2 (moderate contamination) and 3 (substantial contamination, possibly impeding water intake).

Feed intake was measured as the difference of feed offered and leftover. Because it was noted during the first adaptation period that guinea pigs preferred parsley stalks over parsley leaves, stalks and leaves were weighed separately. To account for evaporation losses, additional samples of parsley stalks and leaves were placed in the same room on a daily basis. To account for evaporation losses in faeces, opportunistic samples of freshly defecated faeces were collected for each animal during each metabolism cage period and weighed separately. For the calculation of faecal water losses, the water content of these freshly defecated faeces was assumed for the total amount of defecated faeces.

Representative samples of diet items (collected daily during each metabolism cage period) and the complete leftovers and faeces were dried at 60 °C to constant weight and ground (1 mm, Retsch Mühle, Retsch GmbH, Haan, Germany). Urine was sealed and stored at -21 °C for further analysis. For analysis, thawed urine was stirred vigorously to achieve a homogenous matrix for a representative sample. All samples, including urine, were analysed for dry matter (DM) by drying at 105 °C to constant weight.

Data are displayed as means standard \pm deviation. Statistical analyses were performed in SPSS 21.0 (SPSS, Chicago, IL, USA). Parallel measurements of water intake from nipple drinkers and open dishes during the adaptation periods were not normally distributed and therefore compared within individuals by related-samples Wilcoxon signed rank test. The overall intake from open dishes and nipple drinkers during the metabolism cage measurements were compared within individuals by independent sample *t*-test. General linear models (GLM) were used to assess the effect of diet and drinking system (as fixed factors, including their interaction), and individual animal (as random factor) on various measurements of DM and water intake and excretion, using Sidak *post hoc* tests for diet when the drinking system \times diet interaction was not significant. Two other GLM used faecal and urinary dry matter concentration as dependent variables, respectively, with individual animal as random factor, drinking system and diet as fixed factors, and the ratio of water to dry matter intake as a covariate (and all 2-way interactions of the fixed factors and covariate). Because data were mostly not normally distributed, all GLM were consistently performed on log-transformed data; normal distribution of residuals was confirmed for these models. Because one animal

Table 1 Nutrient composition of the diets provided to guinea pigs (*Cavia porcellus*) offered two different drinking systems

Nutrient		Grass hay	Parsley stems	Parsley leaves	Pellets*	Seed mix†
Dry matter	%	90.9	10.7	16.3	90.6	88.1
Crude ash	% DM	10.0	13.4	13.9	8.0	6.0
Crude protein	% DM	17.1	7.4	21.3	15.4	16.6
Crude fat	%DM	3.0	1.2	2.7	2.7	8.8
Crude fibre	%DM	22.7	18.6	11.4	23.8	7.6
N-free extracts	%DM	47.2	59.4	50.6	50.7	61.0
Neutral detergent fibre	%DM	47.6	28.5	28.2	56.0	22.6
Acid detergent fibre	%DM	26.5	25.0	14.5	25.9	9.9
Acid detergent lignin	%DM	3.0	2.3	4.0	5.1	2.5
Calcium	%DM	0.85	0.96	1.17	0.73	1.00
Phosphorus	%DM	0.38	0.28	0.38	0.52	0.53
Magnesium	%DM	0.30	0.22	0.30	0.45	0.20
Sodium	%DM	0.12	0.23	0.16	0.27	0.29
Potassium	%DM	2.99	5.33	4.62	1.16	0.71

*Cavia Complete, Versele Laga, Deinze, Belgium.

†Vita balance, Meerschweinchen und Hamster, Landi Schweiz AG, Dotzigen, Switzerland.

(animal 11) did not accept the pellets and therefore did not have a full dataset for all diets, it was excluded from all GLM. The average room temperature was never significantly related, either by itself or as covariable in various GLM, with water intake measures (data not shown) and was therefore not included in any model.

The data from this study were added to a data set on dry matter and drinking water intake from the literature, to assess the relationship between the two measures. This was first performed using a simple nonparametric correlation analysis. Because these data did not meet conditions for parametric tests, not even after log transformation, further statistical analyses were performed on this joint dataset using ranked data, in a GLM with dry matter intake as the independent variable, drinking water intake as the dependent variable, study as a random factor and the effect of diet, coded as absence or presence of fresh feed (in the dataset, grass or parsley) and the presence or absence of a hay-only diet, as fixed factors. The significance level was set to 0.05.

Results

All four feeding regimes were accepted by the animals, with the exception of one animal (animal 11) that consistently refused the pelleted diet and was therefore excluded from most statistical analyses. Without exception, all guinea pigs ingested the hay first, regardless of the other diet component. Even animals on the parsley-dominated diet ingested the hay portion first.

As scored on a daily basis for all animals, open dishes in the adaptation compartments were not contaminated in 53% of cases, showed a mild contamination in 33%, moderate contamination in 11% and a substantial contamination (possibly impeding water intake) in 3% of cases.

Measurements of feed and water intake as well as faeces and urine excretion are summarized in Table 2. For both total water and drinking water intake, the standard deviation of the treatment means was larger for the nipple drinkers than for the open dishes on any diet.

During the adaptation periods when both drinking systems were offered simultaneously, all guinea pigs, except for animal 10, clearly preferred nipple drinkers over open dishes (Fig. 1a). The daily drinking water intake was significantly higher from nipple drinkers than from open dishes ($p < 0.001$), except in animal 10 where intake from open dish was significantly higher ($p < 0.001$). During the metabolic cage stages,

Table 2 Mean (\pm SD) water and feed intake, faeces and urine excretion in 10 guinea pigs (*Cavia porcellus*) on different diets and different drinking systems

Diet	Drinking system	Total water intake [g/kg ^{0.75}]	Drinking water intake [g/kg ^{0.75}]	Feed water intake [g/kg ^{0.75}]	Feed dry matter intake [g/kg ^{0.75}]	Hay [% DM]	Faeces [g/kg ^{0.75}]	Faecal dry matter [%]	Urine [g/kg ^{0.75}]	Urine dry matter [%]
Hay <i>ad libitum</i>	OD	119.8 \pm 48.3	115.1 \pm 48.2	4.7 \pm 0.9	47.0 \pm 9.4	100	45.2 \pm 15.9	35.6 \pm 5.1	34.6 \pm 25.9	10.1 \pm 3.9
	ND	125.6 \pm 59.0	120.6 \pm 58.0	5.0 \pm 1.1	49.1 \pm 11.0	100	45.2 \pm 11.2	36.8 \pm 4.8	32.0 \pm 21.7	10.2 \pm 2.8
Fresh Parsley	OD	211.1 \pm 66.5	30.1 \pm 35.9	180.9 \pm 66.7	34.2 \pm 10.3	20.9 \pm 7.2	21.0 \pm 6.6	30.9 \pm 3.9	88.3 \pm 41.1	4.2 \pm 1.1
	ND	230.5 \pm 68.6	50.6 \pm 37.2	179.9 \pm 52.6	34.1 \pm 8.5	20.4 \pm 4.9	21.3 \pm 8.5	31.1 \pm 4.2	109.2 \pm 42.4	3.8 \pm 1.1
Pellets	OD	109.5 \pm 47.4	101.8 \pm 47.0	7.7 \pm 2.1	45.5 \pm 11.4	14.4 \pm 4.3	50.4 \pm 11.5	44.7 \pm 5.8	31.5 \pm 30.6	9.9 \pm 4.0
	ND	146.0 \pm 97.9	138.0 \pm 97.5	8.0 \pm 1.3	47.4 \pm 7.4	13.5 \pm 1.9	54.6 \pm 11.5	47.0 \pm 9.7	55.1 \pm 69.3	8.0 \pm 5.3
Seed mix	OD	67.8 \pm 37.4	63.6 \pm 36.7	4.3 \pm 1.2	30.8 \pm 9.8	21.8 \pm 6.3	21.2 \pm 9.7	36.5 \pm 4.6	19.5 \pm 21.0	7.9 \pm 4.9
	ND	134.4 \pm 86.9	130.5 \pm 86.4	3.9 \pm 1.3	31.4 \pm 6.7	22.4 \pm 5.3	20.9 \pm 4.7	35.1 \pm 7.2	69.0 \pm 63.8	5.1 \pm 4.8

OD, open dish; ND nipple drinker.

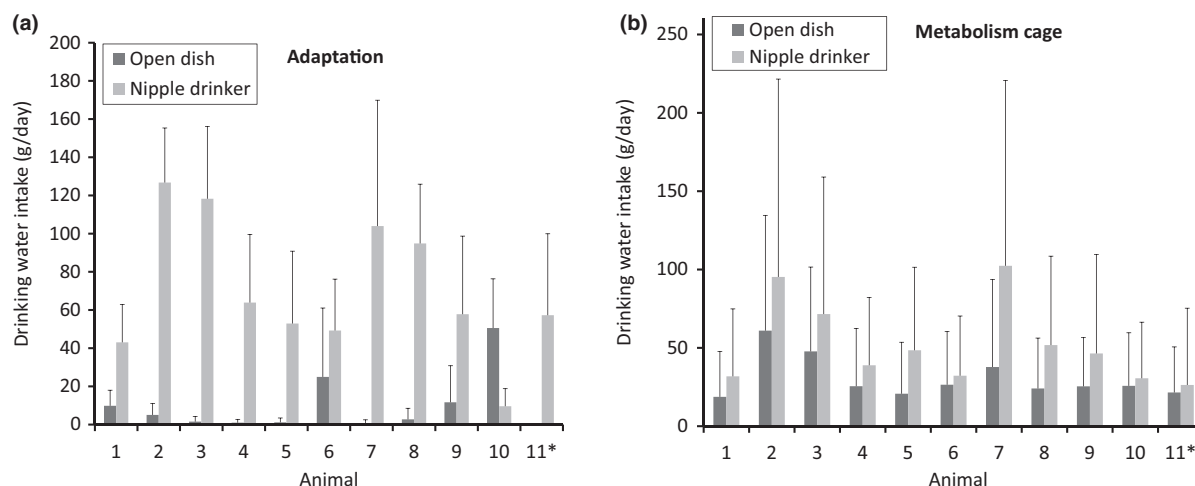


Fig. 1 Mean (\pm SD) drinking water intake in 11 individual guinea pigs (*Cavia porcellus*) in (a) adaptation enclosures with simultaneous access to open dishes and nipple drinkers and (b) metabolism cages where diets were offered twice in random sequence with an open dish and a nipple drinker. All animals received four different diets in random order. Differences between drinking systems were significant for all animals in (a), and for all animals except 6, 10 and 11 in (b). *Animal 11 did not accept one of the four diets and was excluded from further analyses.

drinking water intake was numerically higher from nipple drinkers in all animals; this difference was significant in most animals, except for animals 6, 10 and 11 (Fig. 1b). In the adaptation period, there was a significant difference in drinking water consumption between diets (Fig. 2, Table 3); drinking water intake was lower on parsley than on the other diets.

Individual animal was always significant as a random factor during the metabolism cage period (Table 3). Neither dry matter intake nor feed or water

intake differed between the periods with different drinking systems (Table 3); both measures, however, were significantly different between diets, with lowest values for the seed mix, and the highest dry matter intake on hay, and the highest feed water intake on parsley (Table 3). The drinking water intake was significantly higher with nipple drinkers, and significantly lower on parsley than on the other diets (Table 3, Fig. 3a). The only diet for which drinking water intake was similar on both drinking systems was the hay-only diet (Fig. 3a); in spite of this difference to the other diets, the drinking system \times diet interaction was not significant (Table 3). Total water intake showed a similar pattern. In this case, however, the drinking system \times diet interaction was significant (Table 3); total water intake was similar for both drinking systems on hay, but numerically higher for the nipple drinker on the other diets, and particularly high on the parsley diet (Fig. 3b). The ratio of water to dry matter intake showed a similar pattern as the total water intake, with a significant drinking system \times diet interaction (Table 3), comparable values for both drinking systems on hay and numerically higher values for nipple drinkers on the other diets (Fig. 3c).

The daily faecal water excretion did not differ between the drinking systems and was significantly lower on the seed mix and parsley than on the pellet and the hay diets (Table 3, Fig. 4a), most likely due to the higher feed intake on the latter two diets (Table 2). The faecal dry matter concentration did not differ between drinking systems, but was significantly lower on parsley and significantly higher on pellets

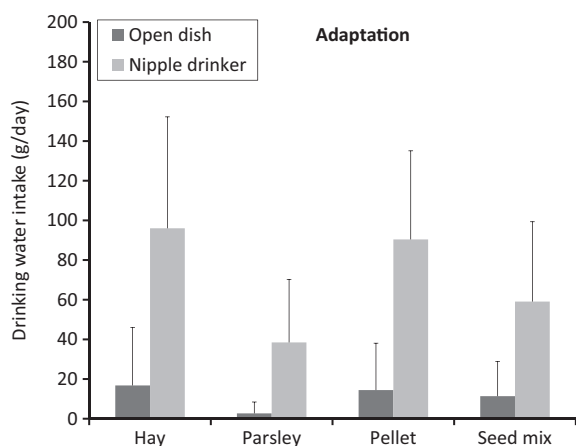


Fig. 2 Mean (\pm SD) drinking water intake on four different diets in 10 guinea pigs (*Cavia porcellus*) in adaptation enclosures with simultaneous access to open dishes and nipple drinkers. Drinking water intake was significantly higher from nipple drinkers, and significantly lower on the parsley diet than on the pellet and the hay-only diets (statistics in Table 3).

Table 3 Results of general linear models (log-transformed data) of the influence of drinking system and diet on different measures in 10 guinea pigs (*Cavia porcellus*) with four different diets and *ad libitum* water access

Dependent variable	Random factor		Within-subjects effects						
			Drinking system		Diet		Interaction		Diets*
Adaptation period									
Drinking water intake (g/kg ^{0.75} /d)	F = 1.56	p = 0.148	F = 57.04	p < 0.001	F = 4.45	p = 0.007	F = 2.21	p = 0.095	Pa≤S=Pe=H
Metabolism cage period									
Dry matter intake (g/kg ^{0.75} /d)	F = 4.02	p < 0.001	F = 0.66	p = 0.420	F = 23.58	p < 0.001	F = 0.04	p = 0.990	S=Pa<Pe=H
Total water intake (g/kg ^{0.75} /d)	F = 8.37	p < 0.001	F = 10.45	p = 0.002	F = 29.65	p < 0.001	F = 3.11	p = 0.033	–
Drinking water intake (g/kg ^{0.75} /d)	F = 4.25	p < 0.001	F = 9.20	p = 0.004	F = 25.79	p < 0.001	F = 1.94	p = 0.132	Pa<S=Pe=H
Feed water intake (g/kg ^{0.75} /d)	F = 3.66	p = 0.001	F = 0.03	p = 0.872	F = 1034.3	p < 0.001	F = 0.54	p = 0.655	S=H<Pe<Pa
Water:dry matter intake (g/g)	F = 6.10	p < 0.001	F = 8.67	p = 0.005	F = 47.88	p < 0.001	F = 3.48	p = 0.021	–
Faecal water output (g/kg ^{0.75} /d)	F = 3.64	p = 0.001	F = 0.10	p = 0.749	F = 43.72	p < 0.001	F = 0.04	p = 0.990	S=Pa<Pe=H
Faecal dry matter content (%)	F = 4.29	p < 0.001	F = 0.09	p = 0.760	F = 32.32	p < 0.001	F = 0.53	p = 0.666	Pa<S=H<Pe
Urinary output (g/kg ^{0.75} /d)	F = 8.79	p < 0.001	F = 11.64	p = 0.001	F = 24.07	p < 0.001	F = 4.29	p = 0.008	–
Urinary dry matter content (%)	F = 5.14	p < 0.001	F = 5.47	p = 0.023	F = 11.93	p < 0.001	F = 2.25	p = 0.091	Pa=S<Pe=H

S, seed mix; Pe, pelleted diet; Pa, parsley; H, grass hay; *compared by Sidak *post hoc* tests; Significant results are set in bold.

compared to the other diets (Table 3, Fig. 4b). Urine excretion was similar for both drinking systems on the hay diet, but numerically higher with nipple drinkers for the other diets (Fig. 4c). The drinking system × diet interaction was significant (Table 3), and the highest urine output was measured on the parsley diet. The urinary dry matter concentration was highest on hay and lowest on parsley (Table 3, Fig. 4d), and significantly lower on nipple drinkers. Although this difference was not evident on the hay diet, the drinking system × diet interaction was not significant in this case (Table 3).

In the GLM relating faecal dry matter concentration as dependent variable to the ratio of water to dry matter intake, the individual animal was the only significant factor ($F = 4.145$, $p < 0.001$); all other factors, covariates or interactions were not significant. In the GLM relating urinary dry matter concentration as dependent variable to the ratio of water to dry matter intake, both the individual animal ($F = 2.772$, $p = 0.009$) and the water:dry matter ratio ($F = 154.382$, $p < 0.001$) were significant, without significant effects of drinking system, diet or any interaction.

When adding the results of this study on dry matter and drinking water intake to literature findings, it is evident that there is a large scatter in the data (Fig. 5). There was a positive nonparametric correlation in this data, irrespective of whether fresh feed was included ($\rho = 0.29$, $p = 0.005$) or excluded ($\rho = 0.26$, $p = 0.019$). In the GLM, only study ($F = 9.016$, $p < 0.001$) and whether feed was fresh or dry ($F = 19.921$, $p < 0.001$) had a significant influence. Neither dry matter intake ($F = 2.226$,

$p = 0.139$) nor whether feed consisted of hay only ($F = 0.614$, $p = 0.436$) had a significant effect. This latter fact did not change when diets with fresh feed were excluded from the analysis.

Discussion

The present study demonstrates a clear influence of the choice of drinking system and feeding regimes on water intake and subsequent urine production and dry matter content in guinea pigs. Because the throughput of fluid through the urinary tract is an important determinant of the susceptibility to urolithiasis, these results facilitate husbandry recommendations for guinea pigs aimed at reducing the prevalence of urolithiasis.

All four feeding regimes were accepted by the animals, with the exception of one single individual that did not accept the pelleted diet. Nevertheless, we observed that all animals completely ate the hay ration first before starting with the main feed. This preference for hay corresponds to the natural diet of guinea pigs, which consist mainly of various grasses (Guichón and Cassini, 1998). Grass hay is generally recommended as staple diet item for guinea pigs and should always be available *ad libitum* (Clauss, 2012; Quesenberry et al., 2012). However, given the fact that guinea pigs do not show particular adaptations to water scarcity (Dicker and Heller, 1951; Dutch and Brown, 1968), constant adequate water provision along with dry feed is imperative.

Literature recommendations for the ratio of water to dry matter intake in guinea pigs are 2–3 ml/g (Wolf et al., 2008; Hagen et al., 2014). A restriction of water

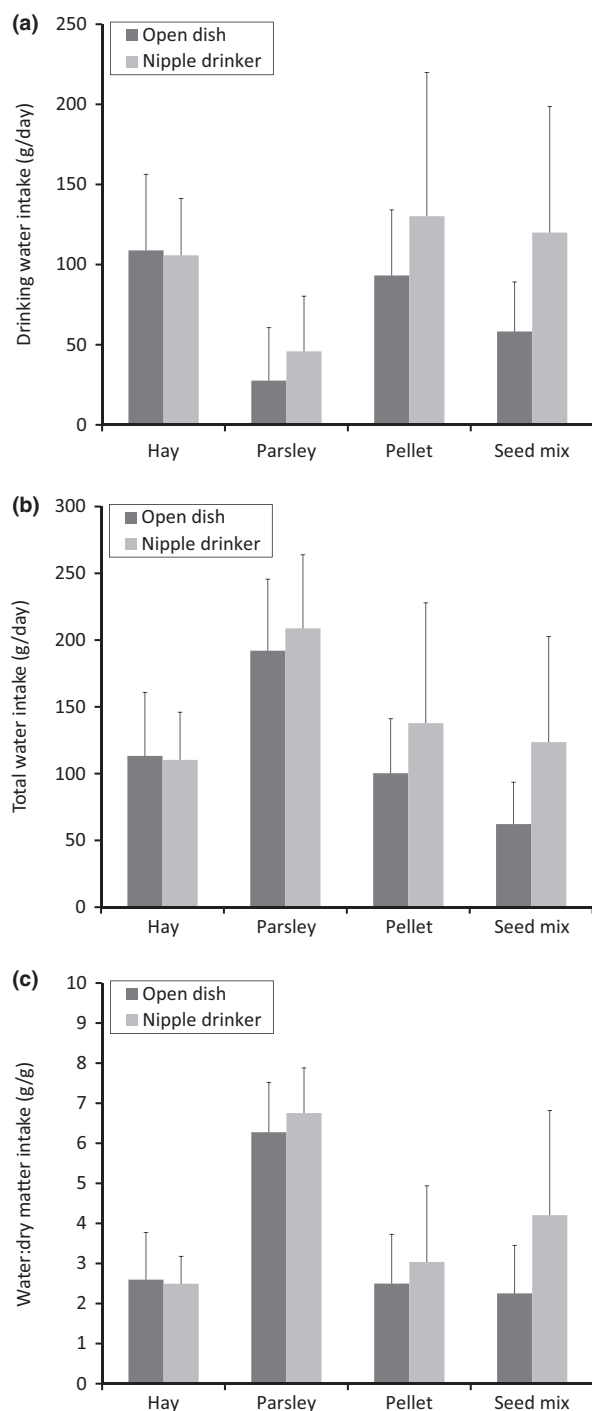


Fig. 3 Mean (\pm SD) (a) drinking water intake, (b) total water intake and (c) the ratio of water to dry matter intake in 10 guinea pigs (*Cavia porcellus*) on four different diets and two drinking systems. Statistics in Table 3.

can lead to a reduction of feed intake (up to 29% in guinea pigs) and nutritional status of an animal (Hirsch, 1973; Coenen and Schwabe, 1995). Such

recommendations assume a linear relationship between water and dry matter intake. However, in the present study, no such linear correlation could be demonstrated when collating data from the literature (Fig. 5). Instead, there was a significant influence of the study from which the data were taken on the relationship. This result was similar to the effect of the individual, which was always significant within the present study. These findings indicate that individual guinea pigs have different drinking habits and that differences between studies – due to different individual animals used, and possibly additionally due to other factors – influence this relationship much more than solely water and dry matter intake. In the present study, the interindividual variation in water intake was more distinct on nipple drinkers than on open dishes. Therefore, investigating the physiologically required water:dry matter ratio might be more reliable with open dishes or other drinking systems that do not lead to a higher water intake than necessary. However, this does not mean that for husbandry purposes, open dishes might be particularly suitable (see below).

Drinking water intake depended on the dry matter content in the feed and was therefore generally low on the parsley diet. Other studies with rabbits and guinea pigs also found a lower drinking water intake with a concomitant higher total water intake when fresh feed was fed (Coenen and Schwabe, 1995; Wolf et al., 1999, 2008; Tschudin et al., 2011b). Nevertheless, total water intake (from feed and drinker) is typically highest on such diets. Therefore, offering fresh feed can be considered a prophylactic measure against urolithiasis. In guinea pigs, fresh feed can also help meeting the requirement for vitamin C (Ediger, 1976). However, offering fresh feed is no justification for not offering drinking water. Even with parsley as a main diet component, the animals of the present study drank some water. Unlimited access to drinking water is strongly recommended (Wolf et al., 2008; Harkness et al., 2013).

In rabbits, drinking water intake has been reported to be particularly high on hay-dominated diets, even when compared to other dry diets (Tschudin et al., 2011b; Prebble and Meredith, 2014). For guinea pigs, no such effect could be demonstrated, neither in the present study itself, nor the study of Wenger (1997), nor in the overall literature data compilation (Fig. 5). Following the speculations of Tschudin et al. (2011b), the difference in the colonic separation mechanism (CSM) between rabbits ('wash back' CSM) and guinea pigs ('mucous trap' CSM, reviewed in Franz et al., 2011) might be responsible for this observation, with

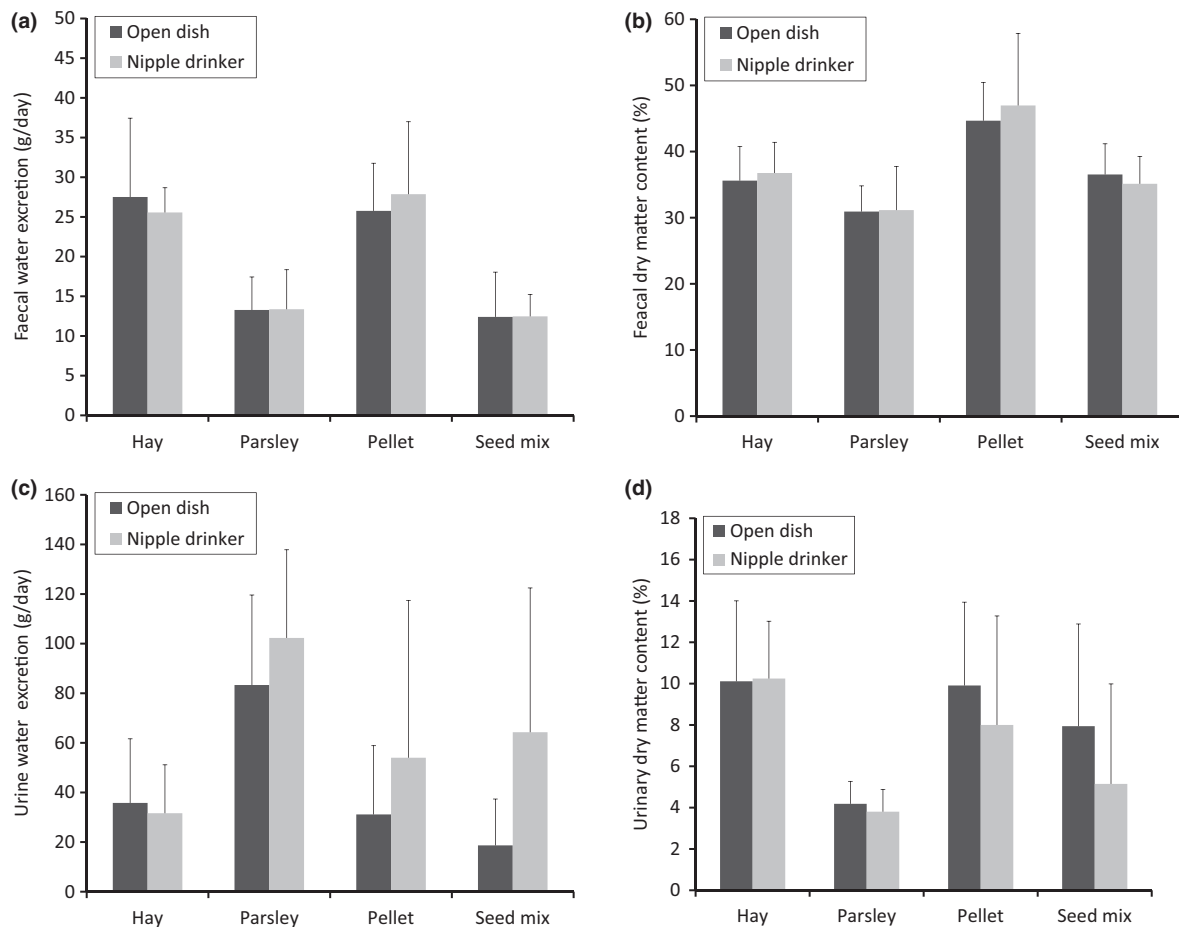


Fig. 4 Mean (\pm SD) (a) faecal water output, (b) faecal dry matter concentration, (c) urine output and (d) urinary dry matter concentration in 10 guinea pigs (*Cavia porcellus*) on four different diets and two drinking systems. Statistics in Table 3.

rabbits requiring a higher amount of fluid for their specific CSM.

The faecal dry matter content was lowest on the parsley, highest on the pelleted diet and not affected by the drinking system. In contrast, urinary dry matter concentration was lower on the nipple drinkers, indicating that most additionally ingested water is excreted via the kidneys. Urinary dry matter concentrations were higher on hay and the pelleted diet, and particularly low on parsley, emphasizing the prophylactic potential of fresh feed against urolithiasis. The higher faecal dry matter content on the pelleted diet might indicate an effect of a finely ground diet with a higher packing density than chewed hay particles.

All but one of the 11 animals of the present study favoured nipple drinkers over open dishes. Of the animals that completed the whole study, only those two that had the highest open dish water intake when being offered both systems simultaneously during the

adaptation period (animals 6 and 10 in Fig. 1a) had an only numerically but not significantly higher water intake from nipple drinkers (Fig. 1b). For all other animals, the higher water intake from nipple drinkers was significant. In contrast, Hagen et al. (2014) observed that of six guinea pigs, two favoured nipple drinkers, two open dishes and the remaining two had intermediate values. Those animals had originated from the same private breeding facility as those of the present study (without being identical animals). Clearly, of all animals tested so far, the majority preferred nipple drinkers. The contamination of open dishes in the present study was similar to observations in rabbits (Tschudin et al., 2011b) and was not considered to be an important factor in drinking preferences.

In rabbits, regardless of the preference for the open dish drinking system, drinking water intake did not differ between periods where only an open dish or only a nipple drinker was offered without restriction

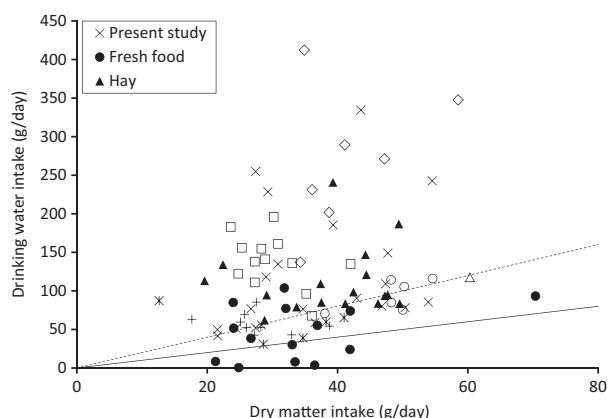


Fig. 5 Data on dry matter and drinking water intake in guinea pigs (*Cavia porcellus*) from the literature – diamonds \diamond (Schröder, 2000), squares \square (Wenger, 1997), triangles Δ (Schwabe, 1995), plus + (Adolph, 1994), minus - (Tau, 1992), circles o (Hagen et al., 2014) – combined with data from the present study. Diets consisting of fresh feed (grass or, in the present study, parsley) are marked separately, as well as diets consisting of hay only. The black line represents a drinking water:dry matter intake ratio of 1:1, the dashed line a ratio of 2:1. Note the absence of a strict relationship between the two measures (see Results for statistics).

(Tschudin et al., 2011b), suggesting that animals were generally drinking to meet water requirements. The preference pattern in the guinea pigs, however, with both a preference for the drinking system that requires to spend more time drinking (Tschudin et al., 2011a), plus a higher water intake from it, suggests the fulfilment of an activity-related oral behavioural motivation linked to a lack of fibre in the diet rather than a thirst-related physiological requirement. This appears all the more evident because the diet typically requiring the highest amount of rodent-specific oral processing – whole hay – was the only one where water intake was similar between the drinking systems (Fig. 3). A hypothesized behavioural motivation for oral processing activity matches the observation that guinea pigs always ingested the hay component of their diets first, regardless of the other diet components.

While apparently no particular stereotypes have been described for guinea pigs (Würbel, 2006), these animals are especially known to have a tendency for playing with nipple drinkers (Ediger, 1976; Harkness et al., 2013), and it has been suggested that a lack of occupation, such as triggered by an energy-dense diet without additional offer of roughage, can lead to polydipsia (Wenger, 1997; Wolf et al., 2008). This may be related to a similarity of the movements of the oral processing apparatus during chewing and drinking from a nipple drinker. The drinking behaviour with nipple drinker has been described as ‘gnawing’

(Harper, 1976). In a detailed study on the jaw movements during nipple drinker manipulation, Gerstner and Goldberg (1989) showed that guinea pigs drinking from a nipple drinker show a typical pattern of vertical gnawing motions and tongue protrusion (i.e. a sequence not typical for chewing) interrupted by a pattern of a combination of vertical and horizontal jaw movements (i.e. a sequence typical for chewing). The suggestion appears plausible that therefore, nipple drinkers can serve as a release for a frustrated gnawing and chewing motivation. The high motivation for guinea pigs for oral manipulation has also been considered the reason for their tendency to chew the fur of themselves or cage mates in the absence of hay, leading to the typical problem of trichobezoars (Gerold et al., 1997). Hay is also considered prophylactic against other potential abnormal behaviours in guinea pigs such as teeth chattering or bar biting (Brandão and Mayer, 2011).

The evident question why a similar motivation for oral activity did not lead to increased nipple drinker use in rabbits (Tschudin et al., 2011a) and the chinchillas and even four of the guinea pigs in Hagen et al. (2014) could lie in a difference of the feeding regime. In both of these studies, the hay component of the diet was always offered *ad libitum*. Therefore, the animals would have been able to accommodate any potential motivation for oral processing behaviour by feeding on hay. Actually, playing with nipple drinkers is listed as a behavioural abnormality in rabbits, likely due to a restricted availability of gnawing material such as hay (Gunn and Morton, 1995; Lidforss, 1997). Therefore, and because fur licking, hair ingestion and trichobezoars have been reported as a husbandry-related behavioural problem associated with a limited offer of hay in rabbits (Beynen et al., 1992; Lidforss, 1997; Berthelsen and Hansen, 1999), it could be speculated that rabbits and chinchillas might also show a different drinker preference if kept without constant access to roughage. Nevertheless, the guinea pigs of the present study preferred the nipple drinkers when provided with grass hay *ad libitum* (Fig. 2). Detailed studies on responses to husbandry-related stress are required to further corroborate, and understand, such differences in behaviour.

Additionally, the body conformation of rabbits and chinchillas may make open dish drinking easier for these species than for guinea pigs. Hence, another possible reason for the lower water intake from open dishes could lie in the physical difficulty for guinea pigs to drink from a dish with an edge of several centimetres. Given the guinea pigs’ low

body height and short legs and neck, obtaining a natural drinking position would appear possible in the case of drinking from an open dish whose borders are at ground level, so that the animals could lower their heads into it. For evident hygienic reasons, such a setup appears unpractical. In the only other study known to the authors that investigated an effect of various dinking system on water intake and performance of guinea pigs, the animals were kept in groups, in a production setting, on a diet of *ad libitum* fresh grass and grass hay and a restricted amount of barley meal (Sánchez et al., 2013). The animals had similar high water intakes (and concomitantly higher weight gains) on either an open dish that was automatically refilled (from an upside-down water storage bottle) or from a nipple drinker system (as opposed to a simple open dish or a suction drinker). Given that the animals most likely were exposed to much more social interactions, and in particular to *ad libitum* grass hay, the results appear similar to the present study. However, the difference between the two open dish systems is interesting, with the one where the water level progressively decreased and putatively made drinking more difficult over time leading to lower

water intake. Studies on the natural drinking position on the guinea pigs are lacking so far.

In summary, nipple drinkers were the preferred drinking system, and water intake was generally higher with this system. No apparent disadvantages of these systems were evident. Therefore, we recommend nipple drinkers for guinea pigs; even though animals should receive both grass hay and fresh forages on a daily basis, the additional behavioural stimulation or outlet offered by nipple drinkers can be considered as behavioural enrichment and a tool to potentially increase water intake.

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